Hipparion sp. (Equidae, Perissodactyla) from Diavata (Thessaloniki, northern Greece)

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Synopsis

Some hipparion remains from Diavata, about 4 km NNW of Thessaloniki, northern Greece, are studied; the locality is known for the giant hyaena *Hyaena salonicae* Andrews. The hipparion is medium to large, and has highly plicated teeth, a large subtriangular protocone, usually multiple 'plis caballins' and an elliptical hypocone with two hypoconal grooves. It represents a form between the primitive hipparions of the Lower Vallesian and the more evolved ones of the Turolian. It belongs to the second *Hipparion* zone of the Mediterranean Neogene, of Upper Vallesian–early Lower Turolian age. No specific name is given because of the small amount of material and the unknown locality.

Introduction

Some hipparion specimens similar to *Hipparion gracile* (Kaup) from the village of Diavata (Dudular), near Thessaloniki, are examined. The material was briefly described by Andrews (1918). The large hyaena *Hyaena salonicae* Andrews is believed to come from the same locality, because of its similar fossilization, but the provenance of the hipparion is more certain ('. . . village Diavata NNW of Salonica . . .') than that of the hyaena ('. . . near Salonica . . .') (Andrews 1918).

There are many papers which discuss the hyaena and its age, but no data concerning the hipparion have yet been published, although they are useful in dating the locality. The hipparion material is described and compared with material coming from the Thessaloniki area (lower Axios valley) and from other Greek and Eurasiatic localities.

Locality

The exact position of the Diavata locality (the old name Dudular has lapsed) is unknown and our efforts to find it are still unsuccessful, because new buildings in the area have changed the terrain. The locality was found in 1917 by Captain Seymour W. Davies, R.A.M.C., who collected the only known material, now stored at the British Museum (Natural History). Information about the site and the deposits are contained in a letter from the collector to Dr L. Fletcher, Director of the BM(NH).

The locality must lie in one of the ravines NE of the village of Diavata between the Gallikos river and the hill Tris Toumbes (Fig. 1). Traces of matrix found on the fossils suggest the fossiliferous bed consists of a yellowish, hard, sandy material, but the collector says in his letter that the fossils occurred in a stiff stratified clay; the fossiliferous deposit is thus most likely a sandy marl. At the bottom of the ravine he said there was a hard (sandy?) conglomerate under the fossiliferous bed, and overlying the fossiliferous bed a series of clay or sand alternating with fine sands or with larger pebbles (Capt. Davies' letter).

The well-known continental neogene deposits of the neighbouring lower Axios valley (Arambourg & Piveteau 1929) consist of three series (Bonis *et al.* 1977, Koufos 1980):

i. a series of yellowish marls, gravels, sands and sandy marls of Dytiko (Upper Turolian),
ii. a series of white-yellow sediments (sandy marls, gravels, sands, marls) of Vathylakkos (Lower Turolian), and

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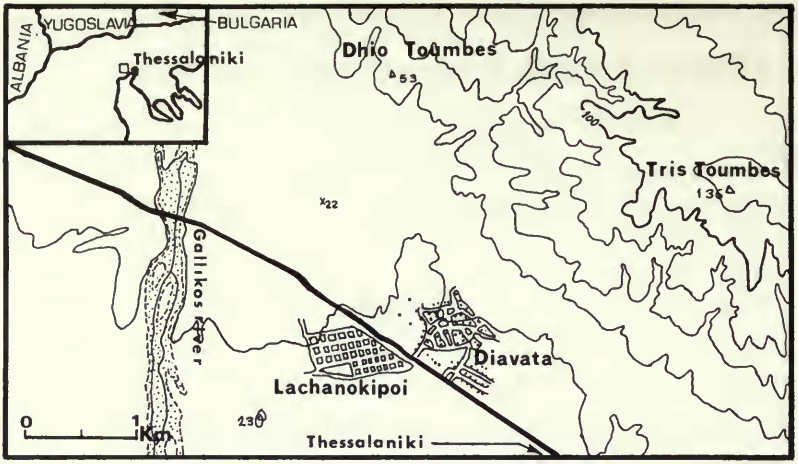

Fig. 1 Map of the Diavata area.

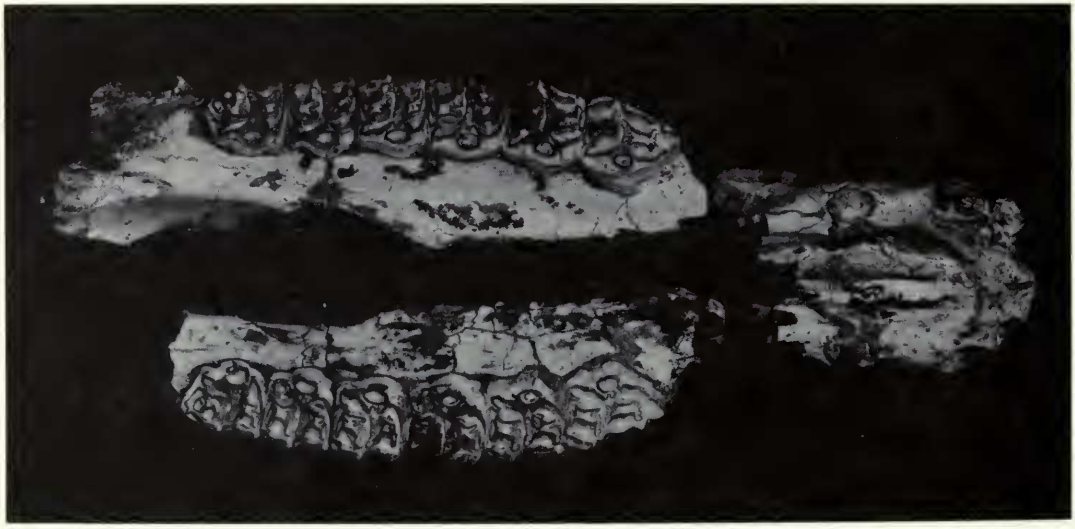

Fig. 2 *Hipparion* sp. BM(NH) M.11585a–c. Diavata, Thessaloniki, Greece. × 0·4. Photo. BM(NH).

Fig. 3 *Hipparion* sp., right maxilla. BM(NH) M.11585a, lateral view. Diavata, Thessaloniki, Greece. × 0·5.

iii. very hard red beds and yellowish marls of Nea Mesimvria (Upper Vallesian–early Lower Turolian).

Thus if Capt. Davies' description of his deposits is accurate they are similar to those of the lower Axios valley. Accordingly the stratigraphy of the locality must be:

i. clay or sand alternating with beds of fine sand or large pebbles,
ii. a yellowish, hard and stratified, sandy marl with the fossils, and
iii. a hard conglomerate, at the bottom of the ravine.

Material and Measurements

All measurements are in mm with estimated values in brackets. Tooth-series length is measured at alveolar level. DAP = anteroposterior diameter; DT = transverse diameter. See also Table 1. Dental nomenclature is according to Sondaar (1961).

1. Right maxilla with P^2–M^3, BM(NH) M.11585a:
   Length P^2–M^3 = 149·0
   Length P^2–P^4 = 79·0
   Length M^1–M^3 = 70·0

2. Left maxilla with P^2–M^3, BM(NH) M.11585b:
   Length P^2–M^3 = 150·0
   Length P^2–P^4 = 80·0
   Length M^1–M^3 = 69·9

3. Portion of premaxillae with left I^2–I^3 and right I^2, BM(NH) M.11585d:
   Width at the border of the incisors = 60·0

4. Portion of premaxillae without incisors, BM(NH) M.11585c:
   DAP I^3–C = 20·9
   Width at the border of the incisors = 61·0

5. Occipital portion of a skull, BM(NH) M.11585e:
   Foramen magnum: Height = 40·0
   Foramen magnum: Width = 29·0
   Max. width between the external surfaces of the condyles = 78·0

6. Proximal part of a radius with remains of diaphysis of the ulna, BM(NH) M.11586a:
   $DT_{prox.}$ = 66·3
   $DT_{prox.\ art.\ surf.}$ = (63)
   $DAP_{prox.\ art.\ surf.}$ = 31·0

7. Distal part of a tibia, BM(NH) M.11586b:
   $DT_{dist.}$ = 61·3
   $DT_{dist.\ art.\ surf.}$ = 50·7
   $DAP_{dist.}$ = 38·5

8. Proximal and distal part of a tibia from a young individual, BM(NH) M.11586c, d.

Fig. 4 *Hipparion* sp., right tooth-series. BM(NH) M.11585a, occlusal view. Diavata, Thessaloniki, Greece. × 0·95.

Table 1 Tooth measurements (mm) in the Diavata hipparion.

Teeth		DAP × DT (occlusal)	DAP × DT protocone	Enamel formula[1]	Protocone shape index[2]
P^2	right	30·0 × 23·6	7·2 × 5·4	4, 8, 5, 2 / 1	75
	left	31·0 × 23·5	7·4 × 5·7	6, 9, 7, 2 / 1	77
P^3	right	24·5 × 25·8	7·6 × 5·1	5, 8, 7, 2 / 1	67
	left	24·5 × 25·3	7·7 × 5·2	3, 10, 9, 1 / 1	67
P^4	right	25·0 × 25·3	8·0 × 5·6	3, 11, 10, 2 / 3	70
	left	24·9 × –	8·0 × 5·3	2, 8, 8, 1 / 2	66
M^1	right	20·9 × 23·0	7·8 × 4·8	2, 9, 11, 1 / 3	61
	left	20·7 × 24·1	8·0 × 4·9	2, 9, 13, 2 / 5	61
M^2	right	21·2 × 23·0	7·9 × 4·9	3, 10, 9, 2 / 2	62
	left	21·5 × 24·0	8·0 × 4·8	2, 8, 11, 2 / 2	60
M^3	right	24·8 × 21·6	7·8 × 4·5	3, 7, 7, 4 / 3	58
	left	25·2 × –	7·5 × –	4, 7, 8, 3 / 2	–

[1,2] Gromova (1952).

Description

The two maxillae studied do not preserve large parts of the skull. The crista facialis of the right maxilla is well preserved; its anterior end is above the M^1 and its distance above the alveolus of the M^3 is 41·0 mm. The teeth are well preserved except for the P^4, M^1 and M^3 of the left maxilla, which are partly destroyed. The wear of the teeth is at the end of the second stage or beginning of the third (Gromova 1952).

P^2: Small with a short anterostyle relative to length. The fossettes are closed, unconnected and highly plicated along their front and rear borders; the plications in their borders are not very deep and the enamel is thin. The 'bouclé prefossette' is multiplicate. The protocone is elliptical and connected with the protoloph. The hypocone is elliptical and has a hypoconal groove which is narrow and deep distally and rudimentary lingually. The 'pli caballin' is simple and well developed.

$P^{3,4}$: The fossettes are unconnected, closed and with high enamel plication. The 'bouclé prefossette' in the right P^4 is separated as an islet. The protocone is large, subtriangular and

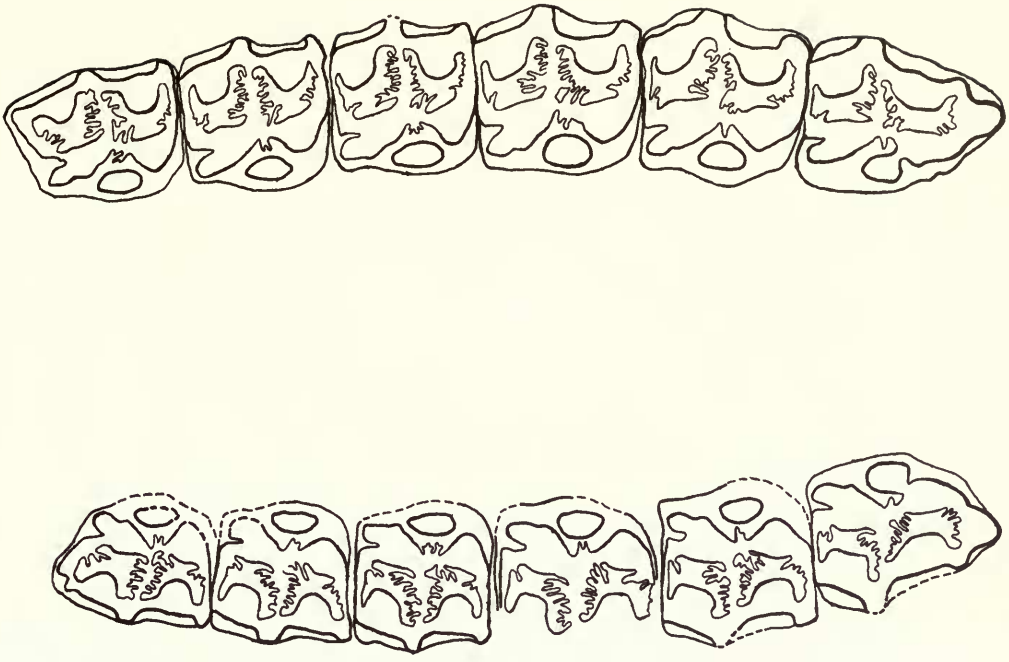

Fig. 5 Tooth-series of the Diavata *Hipparion*. × 0·85.

isolated from the protoloph. The 'pli caballin' is simple in the P^3, and double or triple in the P^4. The hypocone is elliptical and angular posteriorly with two hypoconal grooves.

$M^{1,2}$: These are smaller than the premolars but with the same morphology. The prefossette of both the M^2 is open at the 'bouclé prefossette', which has almost disappeared. The protocone is elongated, subtriangular and isolated from the protoloph. The 'pli caballin' is multiple in the M^1 and double in the M^2. The hypocone is like that in the $P^{3,4}$.

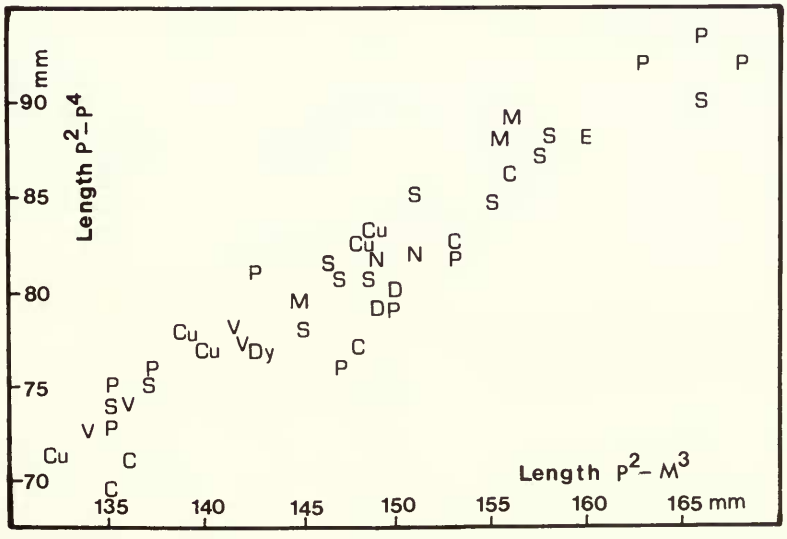

Fig. 6 P^2–P^4 length plotted against P^2–M^3 length. C: Concud, Cu: Cucuron, D: Diavata, Dy: Dytiko, E: Eppelsheim, M: Maraghe, N: Nea Mesimvria, P: Pikermi, S: Samos, V: Vathylakkos.

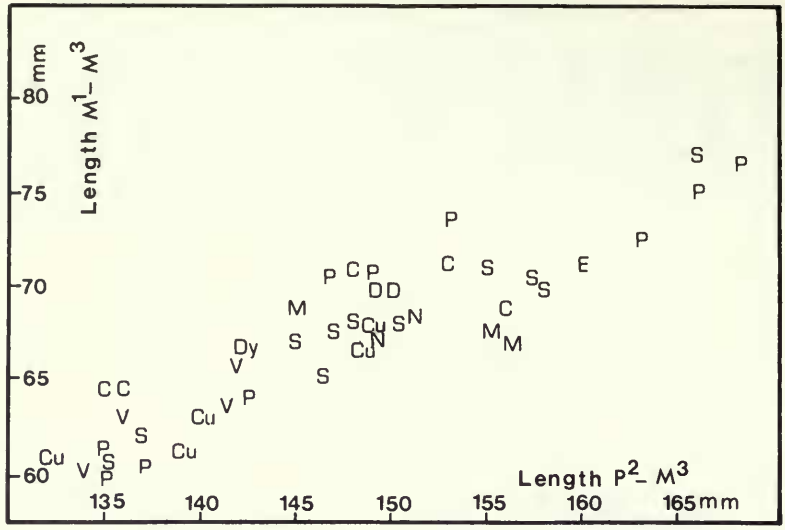

Fig. 7 M^1–M^3 length plotted against P^2–M^3 length. Symbols as in Fig. 6.

M^3: The morphology is comparable to that of the other teeth, but the 'pli caballin' is double or triple and the hypocone is almost round with two well-developed hypoconal grooves. In the left M^3 there is an enamel islet near the 'bouclé prefossette'.

Metrical comparison

A comparison of the present material with that from other localities is given in Figs 6–7. Measurements on teeth of the second and third wear stages were used for all the diagrams because the teeth of the maxillae in the present material are between these stages; the tooth dimensions were measured at the occlusal surface. The length of the tooth series was measured at alveolar level.

In the plots of DAP P^2–M^3 against DAP P^2–P^4 and of DAP P^2–M^3 against DAP M^1–M^3 (Figs 6–7), the Diavata material falls in the middle of the ranges, between the large-sized hipparions (Eppelsheim, large form of Pikermi) and the small ones (Vathylakkos, Dytiko, Cucuron, small form of Pikermi). The Diavata hipparion has an average size similar to the RZO ('Ravin des Zouaves', Axios valley; see p. 342) and Concud hipparions.

Dimensions of individual teeth are compared in Figs 8–11. The material studied is relatively closer to the large and primitive forms of *Hipparion* than to the typical Turolian ones. The tooth dimensions are near those of the hipparions of RZO, Concud and the minimum values of those of Eppelsheim.

Discussion

A well-known Vallesian hipparion is that of Eppelsheim which represents the more primitive form of *Hipparion* (Lower Vallesian). The Eppelsheim hipparion is larger and with more plicated teeth than the Diavata one. Among the Vallesian hipparions there are forms of medium size, with moderate enamel plication and more slender bones than the type of *H. primigenium* (Meyer). Two forms, one of medium size and the other fairly large, are present at the Upper Vallesian locality of Masia del Barbo (Spain), confirming a decrease in the size of *Hipparion* during the Vallesian. A medium-sized hipparion, named *H. depereti* Sondaar, is known from the Upper Vallesian localities of Montredon and Soblay (France). Its teeth

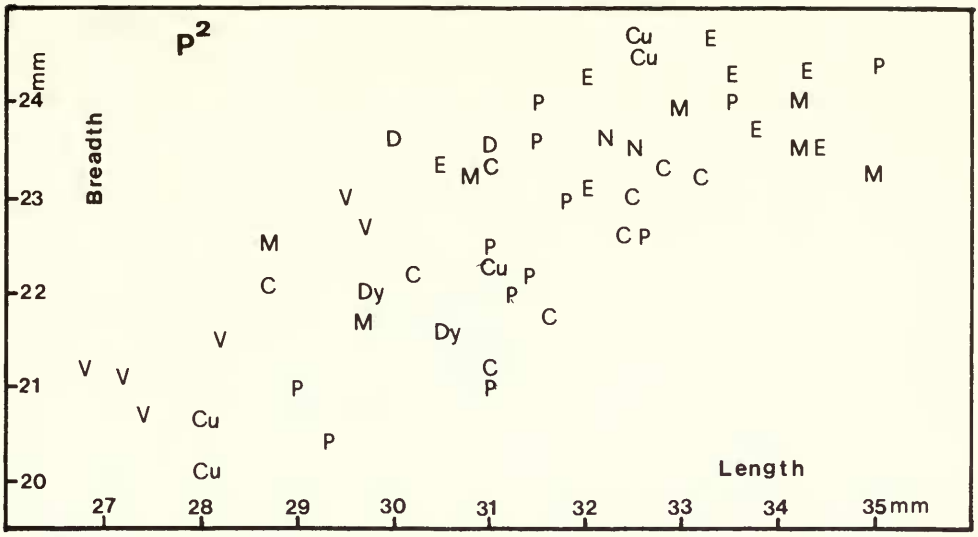

Fig. 8 Tooth breadth plotted against tooth length in P^2. Symbols as in Fig. 6.

are highly plicated, but not so much as in *H. primigenium*, and with ellipitical protocone free from the protoloph, multiplicate 'bouclé prefossette', multiple 'plis caballins', and elliptical hypocone with two hypoconal grooves (Sondaar 1974). All these characters are similar to those of the Diavata material and the dimensions are about the same.

The following Vallesian–Turolian subspecies of *H. primigenium* (Meyer) are known from Spain (Alberdi 1974, Pirlot 1956, Sondaar 1961): *H. p. primigenium, H. p. koenigswaldi*

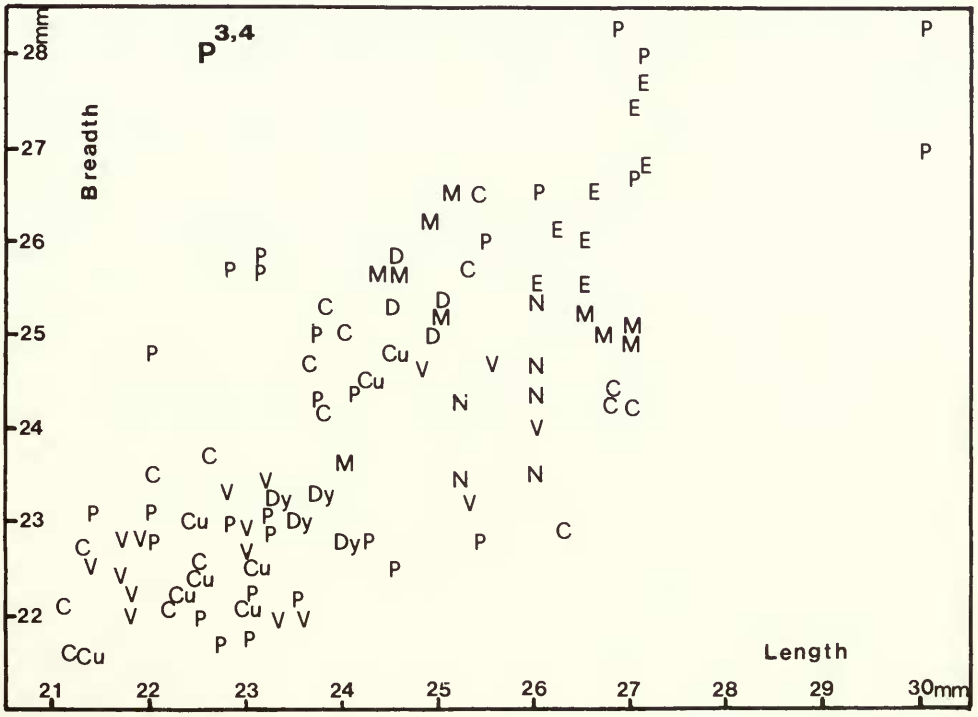

Fig. 9 Tooth breadth plotted against tooth length in $P^{3,4}$. Symbols as in Fig. 6.

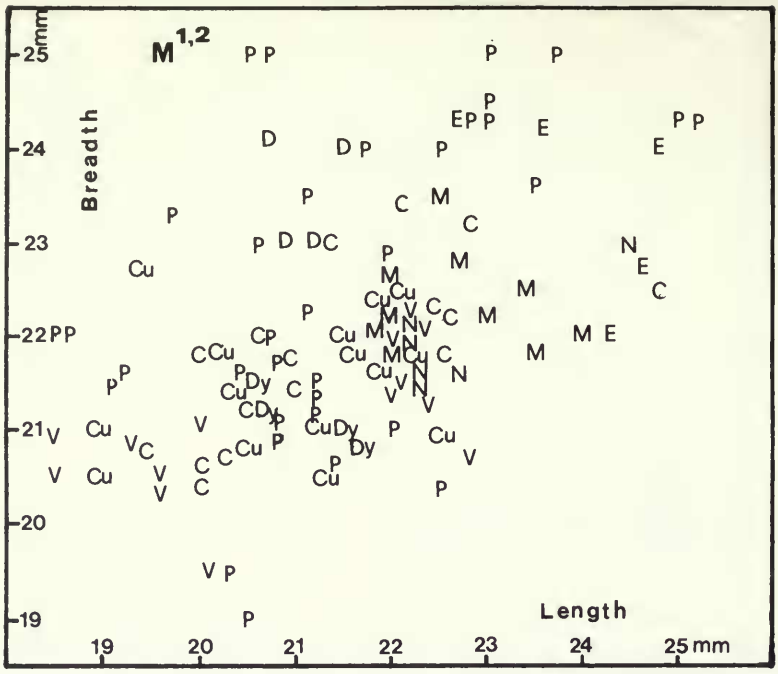

Fig. 10 Tooth breadth plotted against tooth length in $M^{1,2}$. Symbols as in Fig. 6.

Sondaar, *H. p. melendezi* Alberdi, *H. p. catalaunicum* Pirlot and *H. p. truyolsi* Sondaar. All are large forms with highly plicated upper cheek teeth, usually with multiple plis caballins, lingual hypoconal groove and oval unconnected protocone. The Diavata hipparion shows some similarities to *H. p. truyolsi*, such as the triple plis caballins, the slight lingual hypoconal groove, the large protocone and fewer enamel plications than in the typical Vallesian forms. This subspecies represents the transition from Vallesian to Turolian (Alberdi 1974).

Hipparion p. melendezi is also close to the present hipparion especially in features of P^2 morphology, such as the confluent fossettes and the elliptical and connected protocone. It represents the more evolved form of *H. primigenium*, living in the Upper Vallesian (Alberdi 1974). Recently it has been studied again and seems to be closer to *H. concudense* Pirlot and the *Hipparion* sp. from Masia del Barbo than to the Vallesian forms of *H. primigenium* (Forstén 1982).

The other form which is close to the Diavata hipparion is the Upper Vallesian *H. p. catalaunicum* Pirlot. It is like the Diavata hipparion in the form of plis caballins, the slight lingual hypoconal groove and in the dimensions of the tooth series (DAP P^2–M^3 = 149·0 mm; Pirlot 1956).

Thus the Diavata hipparion is closely related to the Upper Vallesian–early Lower Turolian forms, especially to *H. p. truyolsi* Sondaar, a transitional type occurring from Vallesian to Turolian.

Hipparions are known dating from the Upper Vallesian to the end of the Turolian from the lower Axios valley. A maxilla (RZO–1) of a large hipparion is known from the locality 'Ravin des Zouaves', near the village of Nea Mesimvria. This specimen is medium to large in size, and has pronounced enamel plication, a small elliptical or round protocone, double or triple 'plis caballins', multiple 'bouclés prefossettes' and robust metapodials. The RZO hipparion is similar to the Diavata one, but it has a smaller protocone on all the teeth, the lingual hypoconal groove is not very deep and is clearly observed in all the teeth except the

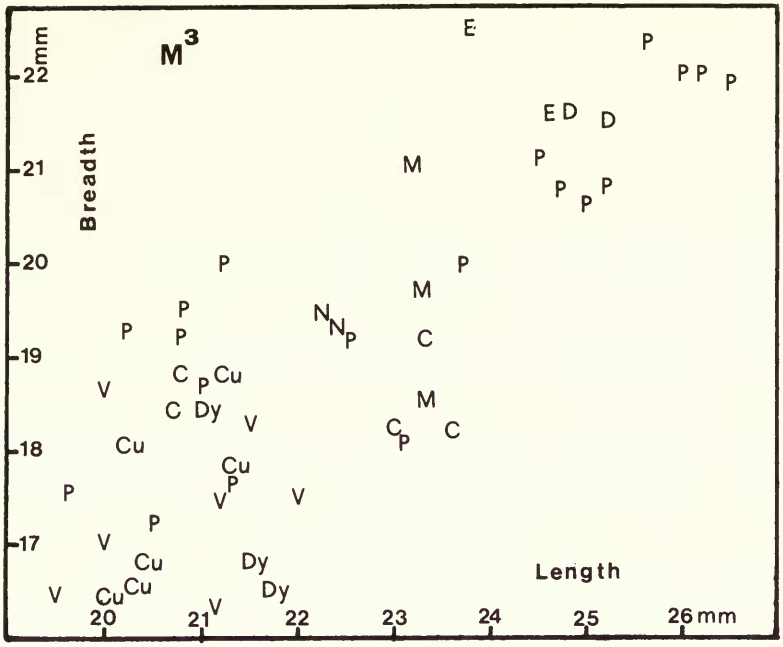

Fig. 11 Tooth breadth plotted against tooth length in M^3. Symbols as in Fig. 6.

M^3, and the 'plis caballins' are less plicated. Another similarity is in the shape of the metacone which is well developed and quadrangular in both specimens. The RZO locality is dated as Upper Vallesian to early Lower Turolian (Koufos 1980).

Two hipparions are known from Pikermi, one large and robust and the other medium-sized and slender. The second form has the characters of the Turolian steppe hipparions, named *H. mediterraneum* (Roth & Wagner). The other has highly plicated cheek teeth, a large subtriangular protocone usually free from the protoloph, two hypoconal grooves and multiple 'bouclés prefossettes'. The Diavata hipparion has smaller dimensions, and less pronounced enamel plication than the large one of Pikermi, which has been named in various ways: *H. brachypus* Hensel (1863), *H. gracile* (Kaup) (Pirlot 1956) and *H. primigenium* (Meyer) (Forstén 1968). The last author noted its relationship to the Eppelsheim hipparion and considered it to represent a Turolian population of *H. primigenium*.

The Turolian hipparions of the lower Axios valley have the characters of the slender, steppe hipparions of this period. They are small to medium-sized with simple to moderately plicated cheek teeth, simple 'bouclé prefossette', usually a small elliptical and isolated protocone, a round and not very large metacone and no lingual hypoconal groove; they thus differ from the Diavata hipparion.

The Diavata hipparion is close in its dimensions to *H. dietrichi* (Wehrli) and *H. proboscideum* Stüder of Samos. The first species is smaller with poor, almost simple, enamel plication, usually a simple 'pli caballin' and an oval protocone which is connected to the protoloph in very worn teeth. The second one is larger with a longer muzzle, moderate enamel plication and a short and wide protocone (Gromova 1952, Sondaar 1971). The Diavata hipparion differs in displaying more primitive characters than the Turolian Samos hipparions.

The above comparisons show that the present species lies between the primitive Vallesian (Eppelsheim) and the more evolved Lower Turolian (Pikermi, Axios valley, Samos)

hipparions, with an observable decrease in size and plication number, representing a reduction in primitive characters from the condition at Eppelsheim.

Diagnosis

The characters of the Diavata hipparion can be summarized as follows:

i. medium to large size
ii. pronounced enamel plication in the upper cheek teeth; large subtriangular and isolated protocone (except on the P^2); usually multiple 'plis caballins', and elliptical hypocone with two hypoconal grooves
iii. morphological and metrical similarities to the more primitive hipparions
iv. differences (lower enamel plication, smaller dimensions) from the typical *H. primigenium* of Eppelsheim.

From the discussion above and its characters the Diavata hipparion must belong among the Vallesian forms. We cannot give it a specific name, however, because of the small amount of material, the unknown locality and the large number of described species at this period.

Age of the locality

The material of the Diavata locality consists only of that studied herein, with the addition of the maxilla of the hyaena mentioned above (p. 335). This is of large size, similar to *Hyaena brevirostris* Aymard and *H. gigantea* Schlosser, but because of some differences in the shape of the P^4 it was named *Hyaena salonicae* and dated as Upper Miocene by Andrews (1918). Later the specimen was studied further and was found to be similar to *Crocuta gigantea* (Schlosser), except for the large protocone on the P^4. Pilgrim (1931) considered it to be a different Pontian species of *Crocuta, C. salonicae* (Andrews). In his study of the Pontian hyaenas Kurtén (1957) identified the one from Diavata as in the subgenus *Percrocuta*, and noted that it possibly belongs to the evolutionary line of *C. gigantea, C. carnifex* (Pilgrim) and *C. grandis* Kurtén, but that it is still different enough in the shape of the P^4 and in dimensions to represent a different species, ? *Crocuta* (? *Percrocuta*) *salonicae*. Beaumont (1979) showed that this maxilla is similar to three different species of different ages, and that it could belong either to the Pontian *Adcrocuta eximia* (Roth & Wagner), the Lower Pliocene subgenus *Pachycrocuta*, or the ? Villafranchian *Hyaena* (*Pachycrocuta*) *brevirostris*. The known hyaenas of the lower Axios valley belong to *Adcrocuta*, and although the collected material is sparse the species *A. eximia* is found in the Turolian localities of the area and a new subspecies *A. eximia leptoryncha* Bonis & Koufos has been described from the Upper Vallesian locality of RPl ('Ravin de la Pluie') (Koufos 1980, Bonis & Koufos 1981). But the Diavata hyaena cannot help to determine the age of the hipparion because its systematic position is unknown and its provenance is uncertain.

The age of the Diavata locality can be estimated, however, using the hipparion material itself. There are two *Hipparion* biozones in the Mediterranean Vallesian (Sen *et al.* 1978). The first (Lower Vallesian) is characterized by a heavy hipparion with archaic dental and locomotor characters. The second (Upper Vallesian–early Lower Turolian) has two forms: one medium-sized and heavy and the other an even more robust form; one is smaller, the other larger than the hipparion of the first zone. The primitive characters persist in these hipparions (Sen *et al.* 1978). The Diavata hipparion is morphologically similar to the more evolved Vallesian forms of *Hipparion* and must therefore belong to the second zone of the Mediterranean Neogene, comprising the period Upper Vallesian–early Lower Turolian. A similar age is possible for the giant hyaena if it indeed comes from the same level as the hipparion. A similar age is estimated for this hyaena by Mme Germaine Petter, Musée National d'Histoire Naturelle, Paris (personal communication).

If our continued efforts to find the locality are successful its discovery will help the positive dating of the locality and deposits.

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